

PROTECTIVE ANT-PLANT INTERACTIONS AS MODEL SYSTEMS IN ECOLOGICAL AND EVOLUTIONARY RESEARCH

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■ **Abstract** Protective ant-plant interactions, important in both temperate and tropical communities, are increasingly used to study a wide range of phenomena of general interest. As antiherbivore defenses “worn on the outside,” they pose fewer barriers to experimentation than do direct (e.g., chemical) plant defenses. This makes them tractable models to study resource allocation to defense and mechanisms regulating it. As multi-trophic level interactions varying in species specificity and impact on fitness of participants, ant-plant-herbivore associations figure prominently in studies of food-web structure and functioning. As horizontally transmitted mutualisms that are vulnerable to parasites and “cheaters,” ant-plant symbioses are studied to probe the evolutionary dynamics of interspecies interactions. These symbioses, products of coevolution between plants and insect societies, offer rich material for studying ant social evolution in novel contexts, in settings where colony limits, resource supply, and nest-site availability are all more easily quantifiable than in the ground-nesting ants hitherto used as models.

INTRODUCTION

In a diverse set of mutualisms, plants are protected, fed, or transported by ants (Beattie 1985). This review deals with ant-plant protection mutualisms, ranging from opportunistic, facultative interactions, in which plants offer food rewards to foraging ant workers, to interactions in which plants also offer hollow structures to nesting ants encouraging more constant association. This latter type of interaction includes a number of specific and obligate symbioses. We cover the spectrum because much has been learned by comparing systems varying in their degree of specialization.

Attracting the attention of naturalists over a century ago (Belt 1874, Rettig 1904, Ridley 1910), these mutualisms have often been considered as interesting, sometimes spectacular, examples of biotic interactions but of limited importance in ecological communities. Recent work, however, suggests that opportunistic ant-plant mutualisms play a key role in structuring food webs in tropical forest canopies. Although restricted to the tropics, symbiotic ant-plant mutualisms involve species of over 100 genera of angiosperms and 40 genera of ants (Davidson & McKey 1993), and they are important components of tropical communities.

Ant-plant protection mutualisms have served as model systems for studying a great range of questions of general interest in ecology and evolutionary biology. In the 1960s, studies of a myrmecophyte symbiosis demonstrated beyond doubt what happened to plants when their defenses against herbivores were removed (Janzen 1966, 1967a,b, 1969). These elegant studies were seminal in stimulating work on plant-animal coevolution in many contexts. Since then, ant-plant protection mutualisms have continued to be tractable systems for testing aspects of plant defense theory (Fonseca 1994, Heil et al. 2002b). Myrmecophyte symbioses have served with increasing frequency as models for examining conditional outcomes in interspecies interactions (Gaume et al. 1998) and understanding the evolutionary stability of mutualisms in the face of potentially destabilizing conflicts (Yu 2001). They have figured prominently in recent work on species coexistence (Palmer et al. 2002, Yu et al. 2001), the structure of food webs (Letourneau & Dyer 1998a,b; Schmitz et al. 2000), and other themes in community ecology. We review recent research, highlight aspects where future research is likely to lead to important advances in our understanding, and show that these systems can serve as material for an even wider range of questions in ecology and evolutionary biology.

NONSYMBIOTIC, “REWARD-BASED” INTERACTIONS (MYRMECOPHILIC INTERACTIONS)

Ants are often among the most important predators of arthropods (Floren et al. 2002, Hölldobler & Wilson 1990, Novotny et al. 1999). Ants attracted by plant-derived food rewards serve as an important indirect defense mechanism of plants in both tropical and temperate communities (Bronstein 1998, Buckley 1982, Davidson & McKey 1993, Huxley & Cutler 1991). These interactions are most commonly facultative, involving opportunistic attraction of ants nesting elsewhere to plant-produced food rewards.

The plant may produce these rewards directly or indirectly. Myrmecophilic (“ant-loving”) plants directly produce food rewards such as extrafloral nectar (EFN) or food bodies. Extrafloral nectaries function in protection and not in pollination (Bentley 1977). They are known in at least 66 families of flowering plants (monocots and dicots) and ferns but are absent in “gymnosperms” (Elias 1983). Food bodies are nutrient-rich cellular structures that can easily be removed by foraging ants; they have been described in at least 20 plant families (O’Dowd 1982).

Other plants lack obvious ant-specialized traits but frequently harbor ant-tended hemipteran trophobionts. Recent reviews of ant-hemipteran interactions are provided by Delabie (2001), Gullan (1997), and Gullan & Kosztarab (1997). Most ant-tended hemipterans are phloem-feeders and excrete excess liquid as sugar-rich honeydew. An important resource for ants, honeydew-producing hemipterans are often monopolized by territorial, ecologically dominant ants (Blüthgen et al. 2000). These generalist predators can strongly reduce densities of phytophagous insects.

Protective Effects of Ants

Many studies have demonstrated protection in facultative ant-plant interactions (Bentley 1977, Koptur 1992). Recent work has greatly extended the evidence for protection by ants opportunistically attracted to plant-derived rewards (Costa et al. 1992, de la Fuente & Marquis 1999, delClaro et al. 1996, Koptur et al. 1998, Oliveira et al. 1999, Sobrinho et al. 2002). EFN-consuming ants can even provide protection in plantations of economically important species such as cashew, *Anacardium occidentale* (Rickson & Rickson 1998), showing the potential of such mutualisms in biological control. In addition to herbivores, plant enemies against which nectary-visiting ants have been demonstrated to defend include leaf-cutting ants (Farji Brener et al. 1992) and fungal pathogens (de la Fuente & Marquis 1999). Although herbivores appear to be the general target of both defending ants and scientists studying these interactions, the last cited example shows that we should broaden our attention to other potential interactors.

Other arthropods also exploit these resources and may have diverse effects on ants or plants. Mites and ladybird beetles visit extrafloral nectaries of many plants (Pemberton 1993, Pemberton & Vandenberg 1993, van Rijn & Tanigoshi 1999) and thus might compete with ants, as do stingless bees (O'Dowd 1979) and certain flies (Heil et al. 2003). Other visitors include ichneumonid and braconid wasps (Bugg et al. 1989, Stapel et al. 1997), jumping spiders (Ruhren & Handel 1999), mosquitoes (Foster 1995), and neuropterans (Limburg & Rosenheim 2001). Like ants, some of these EFN consumers can protect plants against herbivores (Pemberton & Lee 1996, Ruhren & Handel 1999, van Rijn & Tanigoshi 1999), whereas others may act as commensals or parasites.

Several studies failed to find protective effects of EFN-consuming ants (Freitas et al. 2000, Mackay & Whalen 1998, O'Dowd & Catchpole 1983, Rashbrook et al. 1992, Tempel 1983). These examples may constitute exceptions or may simply reflect the great variation in both space and time predicted for opportunistic protection mutualisms (Bentley 1976). Variation in the abundance or species composition of ants, phytophagous insects, or other arthropods competing with ants for extrafloral nectar (Heil et al. 2003, O'Dowd 1979) can lead to variation in protective effects (Barton 1986, Di Giusto et al. 2001, Horvitz & Schemske 1984, 1990).

Abiotic conditions influence herbivore pressure, ant visitation rates, or both (de la Fuente & Marquis 1999, Wirth & Leal 2001). The species-richness of assemblages of ants attracted to food rewards varies geographically, seasonally

(Rico-Gray et al. 1998a), and between day and night (Hossaert-McKey et al. 2001). Plant traits also influence ant assemblages. Interspecific variation in EFN structure and placement among *Passiflora* vines may be related to differences in rates of removal of termite baits by nectary-visiting ants (Apple & Feener 2001). In *Triumfetta semitriloba*, the quantity or quality of EFN secretion was considered to dominate over extrinsic factors in determining ant visitation and its effects (Sobrinho et al. 2002). Extrafloral nectary-visiting ants can respond quickly to changes in EFN flow. *Macaranga tanarius* plants treated with jasmonic acid to increase EFN secretion received significantly more nectary visitors for at least 24 h (Heil et al. 2001c). Therefore, EFN-secreting plants can influence the effectiveness of their indirect defense by controlling amount and/or quality of the nectar secreted (see below).

Functional Ecology of EFN Production

Selection should favor production of defense traits in such a way that the protective benefits are maximized and the costs minimized (McKey 1974). Defense should thus be concentrated on plant parts that are most vulnerable or whose loss would be most costly to the plant. Its peak production should be timed to coincide with the greatest risk of herbivore attack, thus showing variation over the 24-h cycle, across developmental stages of plant parts, and over ontogeny of the whole plant. *Dioscorea praehensilis* produces EFN during only one particular phase of its annual cycle, when the single unbranched, leafless shoot climbs from the forest floor to the canopy. Damage to the meristem during this phase would be particularly costly (Di Giusto et al. 2001). EFN production by many plants shows strong diel variation, but in some species, peak production is crepuscular (Heil et al. 2000a, Wickers 1997), in others nocturnal [e.g., *D. praehensilis* (B. DiGiusto, personal communication)] and in still others diurnal [e.g., myrmecophytic *Acacia hindsii*, see Raine et al. 2002; and myrmecophilic *Leonardoxa* (D. McKey, personal observation)]. This variation indicates that timing of production is not the consequence of some simple, physiological (e.g., source-sink) mechanism but could be shaped by selection pressures peculiar to each plant, e.g., the activity rhythms of its particular herbivores. Herbivores of *M. tanarius*, one species with a crepuscular peak of EFN production, show a marked activity peak at dusk and in the first few hours of darkness (M. Heil, personal observation).

In *M. tanarius*, the rate of EFN secretion is responsive to the rate of removal (Heil et al. 2000a), indicating that plants lower costs by reducing their EFN production when EFN is not removed. More studies are required to check whether this regulatory mechanism is a general one.

Does increased investment by the plant in EFN quality or quantity confer increased protective benefit? EFN consists mainly of aqueous solutions of mono- and disaccharides (predominantly sucrose, glucose, and fructose) usually accompanied by much lower concentrations of amino acids and other compounds (Baker et al. 1978, Dress et al. 1997, Galetto & Bernardello 1992, Heil et al. 2000a,

Koptur 1994, Ruffner & Clark 1986, Smith et al. 1990, Stone et al. 1985). Although water in nectar contributes to ant attraction in desert plants (Ruffner & Clark 1986), most ants prefer nectars that are highly concentrated (Galetto & Bernardello 1992) and rich in amino acids or other additional compounds (Koptur 1994, Koptur & Truong 1998, Lanza et al. 1993, Stapel et al. 1997). Such effects can depend on single compounds. Glycine enhances the attractiveness of glucose solutions to *Camponotus* ants (Wada et al. 2001), and fire ants (*Solenopsis invicta*) even distinguish between diastereomers such as D- and L-GLUCOSE (Vandermeer et al. 1995). Although a positive relation between the number of ants attracted and the effectiveness of defense is intuitively evident, few studies, besides the one using inducibility of EFN secretion (Heil et al. 2001c), empirically demonstrate this relation. Even less is known about how differences in plant rewards influence species identity of attracted ants and how this in turn affects protective benefit. More studies are therefore required to determine whether the protective effect of EFN secretion varies with the quantity and/or quality of EFN.

A variety of studies have indicated that EFN secretion, or amino acid concentrations in EFN, may increase in response to herbivory (Koptur 1989, Smith et al. 1990, Stephenson 1982, Swift & Lanza 1993) and that this reaction does not require herbivore-specific elicitors (Heil et al. 2000a, Wäckers & Wunderlin 1999). However, most of these studies suffered from methodological problems (Heil et al. 2000a), and nothing was known about the underlying signaling pathway. In *M. tanarius*, EFN production represents an induced plant defense that is mediated via the octadecanoid signal transduction cascade (Heil et al. 2001c). The earlier reports (see above), along with more recent studies on cotton (*Gossypium hirsutum*, see Wäckers et al. 2001) and several *Acacia* species (M. Heil, S. Greiner, R. Krüger, unpublished manuscript), confirm that inducibility of EFN flow seems to be a taxonomically widespread phenomenon.

Diversity and Abundance of Extrafloral Nectary-Bearing Plants

Important contributions on the taxonomic, floristic, and ecogeographic distribution of extrafloral nectaries are still being made (Dejean et al. 2000; Fiala & Linsenmair 1995; Fonseca & Ganade 1996; O'Brien 1995; Oliveira & Brandão 1991; Rico-Gray et al. 1998a,b). Extrafloral nectary-bearing plant species are diverse and abundant in several different vegetation types. Nearly one-third of 243 plant species surveyed on Barro Colorado Island in Panama (Schupp & Feener 1991), and 12.3% of the 741 plant species surveyed in Pasoh Forest Reserve in West Malaysia (Fiala & Linsenmair 1995), had extrafloral nectaries. Considerable proportions of EFN-producing plants of the total vegetation, or species pool, were also reported for Brazilian cerrado vegetation (Oliveira & Brandão 1991). In contrast, in a study conducted at Los Tuxtlas station in Veracruz, Mexico, only 3% of the 289 tree species investigated possessed extrafloral nectaries (Ibarra-Manríquez & Dirzo

1990). Further studies are required to document and understand such striking variation among plant communities.

Within communities, frequency of extrafloral nectaries appears to vary among plant life forms. In the canopy of an Amazonian rainforest, many species of epiphytes and lianas produced EFN, but a lower proportion of canopy trees did so (Blüthgen et al. 2000). EFN production appears to be disproportionately frequent in vines, most probably because the connectedness of these plants to the surrounding vegetation allows many arboreal ants easy access to nectaries (Bentley 1981, Di Giusto et al. 2001, Hossaert-McKey et al. 2001).

Many ant species visit EFN-producing plants. Twenty-seven ant species were recorded on extrafloral nectaries of *D. praeheinsilis* (Di Giusto et al. 2001). More than 20 insect species were observed on extrafloral nectaries of *Croton sarcopetalus* (Euphorbiaceae) (Freitas et al. 2000). Thirteen ant species and 42 plant species were involved in 135 pairs of ant-plant associations in the semiarid vegetation of the Zapotitlan valley in Mexico, whereas in the dry coastal tropical lowlands of Veracruz (Mexico), 30 ant species and 102 plant species were involved in 312 associations (Rico-Gray et al. 1998b).

Do Opportunistic Ant-Plant Mutualisms Structure Food Webs?

Recent work in tropical forest ecosystems has suggested a key role of these rewards in shaping the nutritional ecology of tree-dwelling ants and the importance of opportunistic ant-plant mutualisms in structuring entire canopy arthropod communities. Knock-down samples of tree-dwelling arthropods in tropical forests are usually dominated by ants; these predators account for a greater proportion of both individual numbers and biomass than their potential prey (Tobin 1995). This seeming paradox is resolved if many tree-dwelling ants are in fact feeding on plant-derived exudates such as EFN and hemipteran honeydew (Davidson 1997, Delabie 2001, Gullan 1997). A variety of evidence favors this hypothesis, including direct observations and patterns in natural abundance of stable isotopes (Davidson 1997, Davidson et al. 2003) and observations showing that scale insects are far more abundant than indicated by knock-down samples (Dejean et al. 2000).

Davidson (1997) has argued that the abundance of these exudates plays a key role in shaping food-web structure in tropical forest canopies by allowing tree-dwelling ants to evolve energetically costly prey-foraging strategies, in particular when ants are physiologically adapted to feed on resources characterized by a low nitrogen content. This would enable them to reach higher densities, and to maintain prey species at lower densities, than if they depended solely on animal prey. What evidence exists for this last hypothesis? We are aware of no experimental manipulative study of this question. Comparative studies show that ant assemblages vary markedly among plant species and life forms, at least partly in response to types and amounts of resources offered (Blüthgen et al. 2000, Dejean et al. 2000, Hossaert-McKey et al. 2001), but how these differences influence herbivore assemblages remains to be studied.

MYRMECOPHYTIC SYMBIOSES

In over 100 genera of tropical angiosperms, one or more species possess specialized structures for housing ants (Davidson & McKey 1993), encouraging more constant associations. Myrmecophytes offer ants pre-formed nesting sites, or “domatia,” in hollow stems (e.g., *Cecropia*, *Leonardoxa*, *Macaranga*), thorns (*Acacia*), petioles (*Piper*), or leaf pouches (e.g., *Hirtella*, *Maieta*, *Scaphopetalum*, *Tococa*). The more constant, long-lived, and exclusive association allowed when ants are resident in plants has usually led to specialization of both partners. This specialization may include increased rate of resource supply to ants by plants and increased protective efficacy of ants. According to the coevolutionary scenario first developed by Janzen (1966) and supported by a great body of studies, ants that better protect their host tree, and plants that invest more in maintenance of their protective ant colony, should thereby increase their own survival and reproduction.

True myrmecophytic interactions include a number of highly specific and obligate symbioses. Although, overall much less frequent and widespread than facultative protection mutualisms, myrmecophyte symbioses are often conspicuous and ecologically important components of tropical communities, either as dominant components of forest understories (Fonseca & Ganade 1996, Morawetz et al. 1992), as abundant “weeds” in vast areas (Central American *Acacia* myrmecophytes; see Janzen 1974), or as pioneer trees (*Macaranga* and *Cecropia*; see Davies et al. 1998, Ferguson et al. 1995, Folgarait & Davidson 1994, Whitmore 1967). For all these plants, protection mutualisms are an important ingredient of their ecological success.

Protection by Resident Ants—Recent Findings

In general, ants protect their myrmecophyte hosts against a broad range of herbivores (Bronstein 1998). Whereas herbivores have breached many plant chemical defenses, few seem to have evolved successful counter-adaptations against the resident ants of myrmecophytes. Rates of herbivory on ant-free *Tachigali* trees were ten times higher than on inhabited ones, and both rates of apical growth and leaf longevity were strongly increased by the presence of ants (Fonseca 1994). Ant-free leaves of *Leonardoxa* lost 7 to 12 times more leaf area to chewing insects than ant-tended ones, and the resident *Petalomyrmex* ants also protected against sap-sucking insects that reduced leaf expansion (Gaume et al. 1997). Ant-occupied *M. bancana* increased their total leaf area by about 40% within one year, whereas trees from which ants had been removed experimentally lost 80% of their leaf area on average (Heil et al. 2001a). Defensive efficacy in such myrmecophytic interactions appears to be much greater than in myrmecophilic interactions of other *Macaranga* species (Fiala et al. 1989, 1994). African *A. drepanolobium* effectively combines the effects of indirect, ant-mediated defense (resident *Crematogaster*) with direct defense by thorns (Stapley 1998). *Azteca alfari* ants on *Cecropia* (Vasconcelos & Casimiro 1997), and *Pheidole* ants on *Tococa* (Alvarez et al. 2001), defend their hosts against leaf-cutter ants.

Herbivory to stems may be even more costly to the plant than is destruction of the leaves they bear. Protection against stem herbivores has been reported for *Pheidole* inhabiting Costa Rican *Piper* myrmecophytes (Letourneau 1998), for *Camponotus* in *Endospermum labios* in Papua New Guinea (Letourneau & Barbosa 1999), and for *Crematogaster* in *M. bancana* in West Malaysia (Heil et al. 2001a).

The first hint of protection by ants against pathogens was the observation that food body-producing trichilia of *Cecropia obtusa* were covered by a fungus in the absence of ants (Belin-Depoux et al. 1997). Experimental results on protection of myrmecophytes against fungi have now been presented for *Piper* (Letourneau 1998) and *Macaranga* (Heil et al. 1999, 2001a). Because bacterial and fungal pathogens often gain entry into the plant at wound sites (García-Guzmán & Dirzo 2001), protection against phytophagous insects probably also confers strong indirect protection against pathogen attack in many myrmecophytes.

Plant-ants, inhabiting several genera of myrmecophytes, prune epiphytes and encroaching vines and sometimes neighboring vegetation as well (Renner & Ricklefs 1998, Suarez et al. 1997). This behavior benefits ants directly by reducing access to the plant by competing ants (Davidson et al. 1988, Federle et al. 2002, Yumoto & Maruhashi 1999), and indirectly by its beneficial effects on the host (reduced competition for nutrients, water, and light).

Many studies thus demonstrate that myrmecophytes sustain more herbivory when deprived of their resident ants, and a smaller number document protection against pathogens and against competing plants. However, only a few recent studies join the classical work of Janzen (1966) in clearly demonstrating higher survival rates (Heil et al. 2001a), or higher seed set (Letourneau 1998), when ants are present. Hard evidence for lifetime fitness benefits is therefore still scarce and quantifying such benefits will be even more difficult for these often long-lived woody plants.

Sources of Variation

Providing ants with nesting space and food thus ensures long-term interactions with, in many cases, specialized, plant-adapted ants. However, in some myrmecophytes, such as *Conostegia setosa* (Melastomataceae), ant occupancy varies among sites and depends on clone size and microclimatic conditions (Alonso 1998). Several other myrmecophytes also show striking variation in identity of ant (or even other arthropod) occupants (Bizerril & Vieira 2002, Dejean & Djiéto-Lordon 1996). Protection can differ depending on the occupant ant species (Gaume & McKey 1999, Suarez et al. 1997, Young et al. 1997). Amazonian *Maieta guianensis* and *Tococa bullifera* occupied by different ants differed significantly in size, most probably because of differential effects on plant growth (Vasconcelos & Davidson 2000).

However, mature individuals of most obligate myrmecophytes, such as *Acacia*, *Barteria*, *Cecropia*, *Leonardoxa*, *Macaranga*, and *Piper*, are inhabited by only a

restricted number of highly specialized ants. The mechanisms that restrict access, and thereby help to stabilize specific mutualisms, are the subject of active research (see below). However, there may be considerable variation in protective efficacy, due for example to variation in size of the resident colony (Duarte Rocha & Godoy Bergallo 1992, Heil et al. 2001b, Itino et al. 2001b), a factor that itself depends on several internal and external factors (see below).

Trophic Structure of the Symbiosis

Several plant-ants store large amounts of debris (exuviae, dead larvae and workers, remains of arthropod prey) inside domatia, and their host plants often show specific adaptations for efficient nutrient uptake from this debris (Treseder et al. 1995). Although most examples of such “nutritional” mutualisms concern epiphytes, the phenomenon also occurs in some forest-understory treelets, e.g., the melastomes *Tococa* (Alvarez et al. 2001) and *Maieta* (Belin-Depoux & Bastien 2002). However, in most protection mutualisms, the flow of resources appears to be principally from the plant to its resident ants (but see below). Plants feed ants directly by producing extrafloral nectar (*Leonardoxa*, African *Acacia* species), cellular food bodies (*Cecropia*, *Macaranga*, *Piper*), or both (Central American *Acacia* species), or indirectly via hemipteran trophobionts tended by resident ants. Several plant-ants further make use of external, “off-host” food sources. The relative importance of food resources offered directly and indirectly by the plant varies greatly, even among closely related species (Gaume & McKey 2002, Itino et al. 2001b), and can even vary among individuals of a single population.

PLANT-DERIVED FOOD SOURCES EFN is an important plant reward to ants in many myrmecophytes. In *Acacia* (Janzen 1966) and *Leonardoxa* (McKey 2000), nectaries of myrmecophytes are more numerous and more active than those of myrmecophilic congeners. In the most specialized variant of the latter system, EFN is the only known food reward. In other lineages, in contrast, nectar secretion is greatly reduced in myrmecophytes. In *Macaranga*, only the leaf glands of non-myrmecophytic species function as nectaries, and are reduced to hydathodes (i.e., water-secreting glands) in the obligate myrmecophytes (Fiala & Maschwitz 1991).

Food bodies (FB) are ontogenetically derived from pearl body-like emergences (*Cecropia*, *Macaranga*, *Piper*) or leaflet tips (Central American *Acacia*) and can be unicellular (*Piper*) or multicellular. They contain high concentrations of lipids, proteins, and carbohydrates (Fischer et al. 2002, Heil et al. 1998). FBs produced by obligate *Macaranga* (Heil et al. 1998) or *Piper* (Fischer et al. 2002) myrmecophytes are rich in lipids and proteins, whereas those produced by myrmecophilic species mainly contain carbohydrates. FBs produced by myrmecophytes show other striking adaptations for feeding animals, e.g., the presence of glycogen instead of starch in FBs of *Cecropia* (Rickson 1971).

Hemipteran trophobionts are third partners in a large proportion of ant-myrmecophyte mutualisms (Davidson & McKey 1993). Their importance appears

to vary among systems. In some cases trophobionts are essential, either because plants appear to produce no direct food rewards or because these rewards do not supply all nutrients required by the ants. Because of their hidden location within domatia, determining the kinds and amounts of resources trophobionts supply to ants is very difficult, and these aspects are much more poorly known than for direct food rewards (McKey & Meunier 1996). Patterns in *Leonardoxa* occupied by *Aphomomyrmex* ants suggested that ants harvested pseudococcid honeydew but consumed coccids as prey (Gaume & McKey 1998). Such differences seem to have important consequences for costs and benefits of the association to the plant (Gaume & McKey 1998, Gaume et al. 1998) and the ant (Gaume & McKey 2002).

Comparative studies suggest that different types of rewards play complementary roles within systems and different roles among systems. For example, both *Macaranga* and neotropical *Acacia* myrmecophytes house their ants in hollow structures and nourish them by FB production. However, the composition of food bodies differs (protein-rich in *Acacia*, containing both lipids and proteins in *Macaranga*), and this is related to differences in other food rewards (M. Heil, B. Baumann, unpublished data). *Acacia* plants provide their ants with abundant extrafloral nectar. In contrast, nectaries are reduced in most myrmecophytic *Macaranga* species (Fiala & Maschwitz 1991), whose *Crematogaster* associates, unlike the ants in *Acacia*, cultivate scale insects (Heckroth et al. 1999) as a source of carbohydrates and probably also proteins. However, *M. puncticulata* is inhabited by a *Camponotus* rather than by a *Crematogaster* species, and this *Camponotus* does not cultivate scale insects. In contrast to other myrmecophytic *Macaranga*, *M. puncticulata* provides its ants with extrafloral nectar (Federle et al. 1998).

FOOD SOURCES EXTERNAL TO THE PLANT Curiously, only a few specialist plant-ants are recorded to eat phytophagous insects that they kill on the plant (Dejean et al. 2001a,b; Gaume et al. 1998; Sagers et al. 2000). Some plant-ants may gather pollen grains or fungal spores that fall onto the host (Davidson et al. 2003), and others gather detritus (Alvarez et al. 2001, Belin-Depoux & Bastien 2002). Such input of externally derived nutrients into the system might benefit the plant partner as well. An estimated 80% of the carbon in *Azteca* workers' bodies was derived from their *Cecropia* host tree, whereas more than 90% of the plant's nitrogen appeared to come from the ants' debris (Sagers et al. 2000). Nutrient flow seems also to be bidirectional in *Tococa* plants defended by *Pheidole* ants, which consume lipid- and sugar-rich trichomes inside some domatia, and deposit detritus in others (Alvarez et al. 2001). These studies suggest that many "protection" mutualisms may also confer nutritional benefits to plants. Further studies are needed to obtain reliable estimates of the complex resource flows between ant-plants and their plant-ants.

Cost-Benefit Relations

Defenses impose costs if the allocation of limited resources to defense entails negative effects on fitness. Allocation costs are generally thought to be an important

explanation of both genetic variability in constitutive defense traits and the evolution of induced resistance. However, the allocation of resources to defense is often difficult to quantify, chiefly owing to the multiple functions of many defensive traits. Ant-plants are useful model systems to study such costs. Feeding resident ants, and thereby enabling indirect defense, appears to be the sole function of food rewards produced by ant-plants. Compared with direct chemical defenses these food rewards are easy to remove, quantify, and analyze. For FB production by the myrmecophilic *Ochroma pyramidale*, O'Dowd (1980) estimated costs at about 1% of a leaf's construction costs. In contrast, FB production by saplings of the myrmecophyte *M. bancana* amounted to about 5% of total aboveground biomass production (Heil et al. 1997). FB production by this species is limited by soil nutrient content (Heil et al. 2001b) and responds faster to increased soil nutrient supply than does photosynthesis or plant growth (Heil et al. 2002b).

Production of food rewards for ants can also entail "ecological" costs (Tollrian & Harvell 1999) that result from negative effects on some of the myriad interactions between the plant and its environment (Heil 2002). For example, a defense trait may attract, rather than deter, enemies, or have negative effects on mutualists. Most studies of ecological costs of defense by ants have dealt with specialized ant parasites of mutualisms (see below). However, several studies have hinted at ecological costs generated by other interactions. Some vertebrates are attracted to myrmecophytes as rich sources of ant prey and destroy domatia (Federle et al. 1999). Specialized *Dipoena* spiders and *Phyllobaenus* beetles that exploit *Pheidole* ants on *Piper* effectively control the plant's ants and even the population of their *Piper* hosts (Letourneau & Dyer 1998a,b). *Pheidole* ants detect and avoid leaves carrying *Dipoena* webs, and plants with spiders sustained significantly higher rates of folivory (Gastreich 1999). Ecological costs are even more likely in the less specific interactions among EFN-producing plants and ants, since non-ant EFN consumers can compete with ants for rewards and reduce the effectiveness of defense (Heil et al. 2003).

MAXIMIZING NET BENEFITS—THE PLANT'S POINT OF VIEW The key precondition for the coevolutionary reciprocal intensification of protection and nutrition postulated for myrmecophytes (Janzen 1966) is that by investing more in ants, the plant can increase protective benefits (Fonseca 1993). *M. bancana* can increase the size of their resident ant colony by producing higher amounts of FBs (Heil et al. 2001b, Itino et al. 2001b). The size of ant colonies resident in myrmecophytes might also be limited by nesting space (Fonseca 1999), and there is at least one report that domatia can be induced by plant ants (Blüthgen & Wesenberg 2001).

There is considerable evidence that bigger ant colonies better defend their host (Duarte Rocha & Godoy Bergallo 1992, Gaume et al. 1998, Heil et al. 2001b), although additional ants are less likely to add significantly to a large colony's defensive effect than to that of small colonies (Fonseca 1993). There is thus a theoretical optimum investment in ants. That plant production of food rewards for ants may be sensitive to both costs and benefits is suggested by the observation that

FB production by myrmecophytic *Cecropia* growing in a greenhouse was limited by light and nutrient availability (Folgarait & Davidson 1994, 1995), whereas FB production by *M. bancana* was limited by soil nutrient content at the plant's natural growing site (Heil et al. 2001b, 2002b). Plant investment in ants can respond to information about likely benefits. *Piper* myrmecophytes produce FBs only in the presence of their *Pheidole* ants (Risch & Rickson 1981) or of a parasitic beetle that appears to have broken the code (Letourneau 1990). Ant-free *M. triloba* plants produced fewer FBs than inhabited plants (Heil et al. 1997). Whether this response is triggered by FB removal or by the presence of a specific ant colony is unknown. *C. obtusa* produced more Müllerian bodies when inhabited by ants (Belin-Depoux et al. 1997), and experimental studies have shown that FB production rates by *Cecropia* depend on intensity of mechanical removal (Folgarait et al. 1994).

MAXIMIZING NET BENEFITS—THE ANT'S POINT OF VIEW Ants that are obligate inhabitants of specific host plants have an interest in their host's vigor, growth, and survival. Although ant and plant interests as such converge, they are not entirely congruent. First, in Fonseca's (1993) model, increased investment in ants by the plant reaches a point where the protective benefits the latter receives level off. In contrast, benefits to ants could continue to increase substantially with plant investment in them. Do ants have an interest in pushing their resource demands into the range where they become parasites of the plant? The potential for parasitism may be particularly great in those myrmecophytes in which ants obtain food indirectly from the host via hemipteran trophobionts (Davidson & McKey 1993), a process over which the plant may have limited control. By tending trophobionts at densities above what is optimal for the plant, ants can act as parasites, or as less effective mutualists (Gaume et al. 1998). Although plants might "retaliate" by growing more slowly, thereby reducing the flow of benefits to ants (Fonseca 1993), decreased reproductive effort might be a more frequent response.

Because these associations involve horizontal transmission and are formed anew each generation, neither partner has a short-term interest in the reproduction of the other (Wilkinson & Sherratt 2001, Yu 2001). Selection could favor ants that manipulate plants in ways that cause them to invest more in resources that benefit ants, at the expense of the plant's own reproduction. One demonstrated mechanism is castration (Yu & Pierce 1998), which has now been observed for Peruvian *Cordia nodosa* (Yu & Pierce 1998), African *A. drepanolobium* (Stanton et al. 1999, Young et al. 1997), and Amazonian *Hirtella* (Izzo & Vasconcelos 2002). Flowering and seed set divert resources from vegetative growth and thus are likely to reduce the flow of resources from the plant to its ants. The consequences of castration behavior for the production of ant food or for lifetime fitness of the host plants appear not to have been investigated. In some systems, this behavior appears to be facultative. In *M. bancana*, *Crematogaster* ants often attack their hosts' flowers after experimental removal of FB-producing stipules. The behavior thus occurs under conditions of strongly reduced food production (M. Heil, personal observations).

Immediate “retaliation” against castrating parasites may be difficult. When ant associates castrate, mutualism may be maintained by evolutionary shifts in the location of flowers (Yu & Pierce 1998), or of domatia (Izzo & Vasconcelos 2002), so that ants rarely encounter reproductive structures. Even when ants do not attack flowers, pollinator access might be reduced by aggressive ant-guards (Willmer & Stone 1997). In the African *A. drepanolobium*, ants are deterred from young flowers by a volatile signal, perhaps released by pollen (Willmer & Stone 1997). Similar observations were recently made for the Central American *A. hindsii* (Raine et al. 2002) and might be a general phenomenon because plant-ants inhabiting myrmecophytic *Acacia* plants were even repelled by flowers of several non-myrmecophytes (Ghazoul 2001).

Ants can also selfishly manipulate plants by reducing the quantity of resources plants supply. Competitively inferior *Tetraponera penzigi* ants destroy foliar nectaries of African *Acacia* myrmecophytes, reducing the probability of their being replaced by more aggressive ants that require higher rates of resource supply and are more effective mutualists of the plant (Palmer et al. 2002, Young et al. 1997).

Investment by ants in their own reproduction imposes a cost to the plant but confers no immediate, direct benefit. This aspect of the functional ecology of plant-ants has been virtually ignored. Variation in reproductive effort among plant-ants appears to reflect strategies of ants, not manipulation by their hosts. At the colony level, greater allocation to growth and survival (production of workers and, in secondarily polygynous plant-ants, of supernumerary queens; see Feldhaar et al. 2000, McKey et al. 1999) would be favored when increased colony size and/or longevity are likely to be repaid by increased benefits from better-performing hosts, and when new nest sites are limited (cost of dispersal is high). Greater allocation to reproduction (dispersing males and females) would be favored by high probability of mortality of the ant colony due to factors that it cannot control by more effective protection of the host (Gaume & McKey 1999).

Defense Against “External” Enemies of the Mutualism

“Castration” parasites appear to have evolved from mutualistic partners that started to “cheat.” However, parasites can also colonize mutualisms. Janzen (1975) reported that *Pseudomyrmex nigropilosa* inhabits ant-acacias and consumes FBs produced by their hosts without exhibiting the defensive behavior of the plant’s mutualistic *Pseudomyrmex* spp. Similarly, *Cataulacus mckeyi* excludes the effective mutualist *Petalomyrmex phylax* from its *Leonardoxa* host trees (Gaume & McKey 1999). Myrmecophilous caterpillars of several lycaenid butterflies have exploited ancestral mutualistic relationships with ants to become parasites of obligate ant-plant interactions. These caterpillars feed on the ants’ host plant and are attended and protected by the ants, although they clearly damage the host plant (Forster 2000, Maschwitz et al. 1984). Similarly, beetles of the genus *Coelomera* can live and feed on ant-inhabited *Cecropia* trees without being attacked by the ants (Jolivet 1991). *Phyllobaenus* beetle larvae live in domatia of *Piper obliquum*,

where they feed on adult workers and brood of the resident *Pheidole bicornis* ants. If ants are absent, the larvae can also use FBs produced by the plant, and can even induce the production of FBs (Letourneau 1990). A similar system has been reported on *C. obtusa* (Belin-Depoux et al. 1997).

Coevolutionary Specializations

The constancy, intensity and (often) specificity of symbiotic ant-plant associations have led to numerous coevolutionary specializations of each partner. These specializations concern several functional domains.

SPECIALIZATIONS FOR DEFENSE AND ITS ALLOCATION Because the interests of ants and plants are only partly convergent, selection on each may favor traits that enable it to control the flow of resources. However, once the rate of flow is set, selection on both partners favors maximizing protection, because the higher the resource-efficiency of mutualistic benefits, the more each partner can invest in its own current reproduction without reducing its future reproduction by harming the mutualist. Among the ant traits that could be affected by such selection is how the resources invested in the worker force are subdivided among workers, i.e., the evolution of worker size. In some plant-ants, worker size has increased compared with that of their less specialized relatives, whereas in others worker size has decreased (Meunier et al. 1999), and adaptation to the particular suite of herbivores attacking the plant appears to be partly responsible for these divergent specializations (Gaume et al. 1997). Behavioral traits may contribute to the defensive efficacy of the many surprisingly small protective plant-ants. *P. minutula* inhabiting *M. guianensis*, *Allomerus decemarticulatus* ants in *Hirtella physophora*, and *Crematogaster* ants in different *Macaranga* myrmecophytes show very effective mass recruiting systems so that many workers are available when larger herbivores have to be attacked. By focusing their attacks on the most vulnerable parts of the attackers (Fiala & Maschwitz 1990), or by “spread-eagling” of prey (Dejean et al. 2001a,b), these ants can protect despite their small size.

Selection could also favor plant traits that reduce the investment required of the ant colony for functions other than plant defense. Ants inhabiting myrmecophytes must defend not only their host but also their nesting sites and food resources against other ant species. This may require larger worker numbers, or additional resource-consuming activities, such as pruning of encroaching vegetation (Davidson et al. 1988, Federle et al. 2002, Yumoto & Maruhashi 1999) or even more sophisticated ways of “burning bridges” (Palmer et al. 2002) that could be used by competitors. Plant traits that help ants exclude such competitors not only reinforce the specificity of these horizontally transmitted interactions (Davidson & McKey 1993), they could also allow mutualist ants to use limited resources more efficiently in plant defense. Epicuticular waxes produced by some, but not all, myrmecophytic *Macaranga* species form slippery surfaces on which only the adapted specialist ants can walk (Federle et al. 1997). Ant associates of

waxy-stemmed species thus require less territorial defense and exhibit reduced pruning activity and lower worker densities (Federle et al. 2002). Another example of filters is the formation by some ant-plants of prostomata (Brouat et al. 2001a, Federle et al. 2001) or membranous or unlignified spots where ants with appropriate behavior and morphology (sometimes coevolved with that of the prostoma; see Brouat et al. 2001a) can easily open entrance holes.

Selection should also favor ant and plant traits that result in concentration of ant effort on sites where defense is most important and most often required. *Azteca* ants living in *Cecropia* plants, and *Crematogaster* on *Macaranga*, can recognize and recruit to damaged sites associated with herbivory and thus represent an effective locally induced resistance (Agrawal & Dubin-Thaler 1999, Fiala & Maschwitz 1990, Fiala et al. 1989). The same response can be elicited by plant sap, particular components of plant extracts, or commercially available green leaf volatiles (Agrawal 1998, Brouat et al. 2000). Many specialized plant-ants, however, patrol even in the complete absence of enemies. This "constitutive" patrolling activity is often concentrated on young leaves, especially in myrmecophytes whose long-lived mature leaves possess direct defenses (Izzo & Vasconcelos 2002, McKey 1984; but see Fonseca 1994). The proximate cues enabling the preferential patrolling of young plant parts remain to be elucidated.

ACQUIRING THE PARTNER: THE BIOLOGY OF JUVENILE MYRMECOPHYTES The association between ant and plant must be established anew in each successive generation, posing several distinct adaptive problems. The first is the orientation to appropriate host plants by mated foundresses of the mutualist ant. The cues used by plant-ant foundresses to locate hosts are only beginning to be studied. Because nuptial flights are often nocturnal [e.g., in *Petalomyrmex* (L. Gaume, personal communication), in *Barteria*-associated *Tetraponera* (C. Djitéto-Lordon, personal communication), and in *Macaranga*-associated *Crematogaster* (B. Fiala, M. Heil, personal observations)], olfactory cues seem most likely. First hints of a role for chemical cues in host plant recognition (whether by olfaction or by contact chemoreception is not yet clear) have been presented (Inui et al. 2001), but more detailed studies are required.

The second problem is survival, which may be a difficult task for juvenile ant-plants and incipient mutualist ant colonies. Interlopers, predators, stochastic mortality factors, and intraspecific competition among incipient colonies of mutualists should all have their greatest impact on ants or plants at this stage (McKey & Meunier 1996). Plants may have limited resources for ants, and ants may be incapable of providing much protection, so that there is little exchange of mutualistic benefits.

Under these circumstances, when in its ontogeny should the plant begin to produce ant-attractant resources? Although some ant-plants already exhibit myrmecophytic traits as seedlings, others become myrmecophytes only when they become small saplings (Fiala & Maschwitz 1992). Brouat & McKey (2000) suggested that the costs of housing and supporting ants are proportionally greater the smaller

the plant. This may be true not only of food rewards but also of caulinary domatia, which are especially costly in terms of stem allocation early in plant ontogeny (Brouat & McKey 2001, Gartner 2001). Producing domatia and other ant resources early in ontogeny thus will be favored only when ants possess sufficient mutualistic specializations to provide protection even when both the host plant and the ant colony are small (Brouat & McKey 2000).

This example shows the potential of myrmecophytes as models for exploring the evolution of allometry in modular organisms (Preston & Ackerly, 2003) and for investigating the linkages between coevolutionary interactions and the evolution of life histories, in both plant and ant partners.

REDUCED CHEMICAL DEFENSE IN OBLIGATE MYRMECOPHYTES Plant defenses are assumed to be costly, and plants therefore should avoid redundant defenses. That chemical defense is reduced in ant-plants was originally hypothesized by Janzen (1966), who proposed that chemical defense has been lost in ant-acacias. Indeed, a diet containing leaf powder from a non-ant-acacia (*A. farnesiana*) had a much stronger negative impact on growth of caterpillars than a diet using the ant-acacia, *A. cornigera* (Rehr et al. 1973). Foliage of most ant-acacias contains no or only small amounts of cyanogenic glycosides (Seigler & Ebinger 1987). Recent studies have focused on the enzymatic antifungal defense of ant-plants in the genera *Macaranga* and *Acacia* (Heil et al. 1999, 2000b), on condensed tannin content in *Macaranga* (Eck et al. 2001), and on herbivore-deterrent amides in inhabited and ant-free individuals of *Piper cenocladum* (Dyer et al. 2001). It has also been assumed that plants might switch during ontogeny from biotic to chemical defense or vice versa (Fiala et al. 1994, Nomura et al. 2000).

However, unequivocal patterns have been found only in some studies (Dyer et al. 2001; Heil et al. 1999, 2000b). No trade-offs were found for *Endospermum* (Letourneau & Barbosa 1999), and in a study covering three different classes of defensive phenolics in the genera *Acacia*, *Leonardoxa*, and *Macaranga* (Heil et al. 2002a). In some studies support for trade-offs appears weaker than claimed (Eck et al. 2001, Rehr et al. 1973, Seigler & Ebinger 1987). Although the reduced direct defense of obligate ant-plants has been demonstrated in many studies, most studies focusing on distinct chemical defenses have found no clear evidence of the expected trade-offs. The dramatically increased vulnerability of ant-free myrmecophytes to herbivores and pathogens is thus still in search of a proximate explanation (Heil et al. 2002a).

Phylogenies for Testing Hypotheses About Evolution of Ant-Plant Interactions

The taxonomic and ecological diversity of ant-plant symbioses offers great potential for using the comparative method to test hypotheses about the evolution of mutualism (Davidson & McKey 1993). Realizing this potential requires robust phylogenies of the interacting organisms. Several recent studies confirm earlier

conclusions that myrmecophytes have arisen repeatedly (e.g., up to four times in *Macaranga*; see Blattner et al. 2001, Davies et al. 2001). Patterns in the phylogeny of the *Crematogaster* associates of *Macaranga* suggest parallels with those in plants and possible cospeciation (Itino et al. 2001a). In the *Leonardoxa* system, phylogeny of the mutualist ants (Chenuil & McKey 1996) and that of the plants (Brouat et al. 2001b, McKey 2000) suggest a complex history, in which reticulate evolution in plants, local extinctions of ant partners, and colonization of plants by multiple ant lineages all appear to play roles. Application of newly developed microsatellite markers to population genetics and phylogeography of ant associates (Dalecky et al. 2002, Debout et al. 2002) will greatly extend the range of tractable questions about the history of these interactions.

ANT-PLANTS AS MODELS TO STUDY THEORIES ON ANTIHERBIVORE DEFENSE

Empirical tests of theories on plant antiherbivore defense encounter considerable difficulty, because most “defensive” plant traits serve other functions as well, and because precise description of spatial and temporal patterns in the occurrence of direct defenses often requires elaborate chemical analyses. Moreover, low levels of herbivory observed under field conditions may result either from low herbivore pressure or from effective defense, making analyzes of the effectiveness of a given defensive trait extremely difficult. Ants represent an efficient defense mechanism whose location on the plant can be precisely described, allowing studies on the temporal and spatial distribution of defense, and that can be experimentally removed from the plant, allowing tests of their effectiveness. They thus present an elegant model system to test several hypotheses of plant antiherbivore defense.

The optimal defense hypothesis predicts that plant defenses should be concentrated in the most valuable and vulnerable parts of a plant (McKey 1974, Rhoades 1979). In fact, many plant-ants patrol and defend preferably the young leaves, which generally have high potential value to the plant (Harper 1989) and sustain most herbivory (Coley & Barone 1996). In the case of facultative, myrmecophilic interactions, this pattern is mainly caused by patterns in the production of food rewards (such as EFN). However, many ant associates of obligate myrmecophytes patrol preferably the young leaves of their host, often independently of the presence of food rewards (Downhower 1975, Janzen 1972). The concentration of ant defense on young leaves has been reported for *Piper* (Risch 1982), African *Acacia* (Madden & Young 1992), *Tachigali* (Fonseca 1994), *Leonardoxa* (Brouat et al. 2000), *Crypteronia* (Moog et al. 1998), and *Macaranga* (Heil et al. 2001a). There seems to be only one reported exception to the general rule: ants patrol young and mature leaves of *Maieta* with the same intensity, but in this case both age classes were observed to suffer equal herbivore attack (Vasconcelos 1991). In general, plant-ants thus form a defense mechanism whose spatial distribution is consistent with the optimal defense hypothesis.

How should plant defenses respond to variation in resource availability? According to the carbon/nitrogen balance hypothesis (Bryant et al. 1983), the response depends on what particular resources are most limiting. *Cecropia* myrmecophytes produce glycogen-rich “Müllerian bodies” and lipid- and amino acid-rich “pearl bodies.” Folgarait & Davidson (1994, 1995) found that the production of pearl bodies increased under conditions of high nutrient level and low light (which should have contributed to relative excess of nitrogen). Although these results supported the C/N balance hypothesis, production of Müllerian bodies increased at high levels of both nutrients and light. Nutrient effects on toughness and leaf expansion rates were also inconsistent with the predictions of this theory (Folgarait & Davidson 1994, 1995). Similarly, production of the (protein-containing, yet lipid-dominated) FBs of *M. triloba* responds quickly and strongly to increased nutrient supply (Heil et al. 2001b, 2002b), and even FBs of *M. tanarius* (containing nearly no proteins) were produced at higher rates when plants received more nitrogen (M. Heil, A. Hilpert, unpublished data). Results from ant-plant studies are thus representative of many other recent studies of chemical defenses that have failed to support the C/N balance hypothesis, which some authors now regard as definitively “rejected” (Hamilton et al. 2001).

According to the resource availability hypothesis (Coley et al. 1985), “mobile” defenses such as alkaloids or other small molecules impose high maintenance costs due to their high turnover rates, but can be reclaimed from leaves before they are shed. Such defenses are predicted to occur mainly in short-lived leaves of fast-growing plants. Ants can move easily over the whole plant surface and are not shed with leaves. They are thus highly “mobile” defenses (McKey 1984). The fact that ant defenses are most spectacularly developed in pioneer trees is consistent with the resource availability hypothesis, as is the frequent restriction of ant defense to young leaves of understory trees whose long-lived mature leaves appear to have immobile direct defenses (Izzo & Vasconcelos 2002, McKey 1984).

PERSPECTIVES

We have focused on ant-plant interactions primarily from the perspective of individuals and populations interacting at local spatial scales. With the exception of a partial treatment of conflicts between mutualists and the evolutionary stability of mutualisms, we have also paid scant attention to the long-term dynamics of these interactions. Examining these interactions at larger scales of space and time would require another review. We indicate what we perceive as some particularly interesting questions in the micro- as well as in the macroecology of ant-plant symbioses.

1. What forces drive the evolution of trophic structure of myrmecophyte symbioses? Are hemipteran trophobionts, apparently essential partners at the outset of many symbioses, sometimes eliminated as plants attempt to gain

control of resource supply to ants? Patterns in *Leonardoxa* strongly suggest such dynamics (Chenuil & McKey 1996, Gaume et al. 1998, Meunier et al. 1999). Does the diversity of trophic structure in ant-plant symbioses reflect the still poorly explored diversity in the nutritional ecology of tree-dwelling ants (Davidson et al. 2003)?

2. Functioning of ant-plant mutualism requires the flow not only of trophic resources but also of information. What mechanisms underlie the flow of information between partners that is required for the exchange of mutualistic benefits? Several mechanisms regulating the provisioning of food rewards by the plants or guiding the ants' patrolling behavior have already been reported, but the nature of the signals appears unclear in most cases. Contemporary methods in chemical and molecular ecology are likely to provide efficient tools to investigate the signals involved in host-finding by founding ant-queens, the mechanisms involved in the restriction of many plant-ants to one or only a few host(s), the regulation of food body production and extrafloral nectar secretion, the diversion of defending ants from flowers, and many other aspects of these interactions.
3. Do conflicts between mutualists drive the evolutionary dynamics of ant-plant symbioses, as current work suggests (Izzo & Vasconcelos 2002, Yu 2001, Yu & Pierce 1998)? Or is evolution of these mutualisms driven by "Red King" mechanisms, in which "the slowest runner wins the coevolutionary race" (Bergstrom & Lachmann 2003)? Interactions of long-lived plants with shorter-lived ants might offer the asymmetry in evolutionary rates that appears to favor such dynamics.
4. How do inclusive-fitness models modify expectations about life-history evolution in plant-ants? How do coevolutionary pressures influence ant social evolution? If selection acts at the colony level, association with a long-lived host that benefits from protection should favor colonies that invest in survival to maximize their future reproduction, and life history of the ant colony should be tied to that of the tree in such a way that their interests tend to converge. However, an ant colony is a society in which individuals both cooperate and conflict. One focus of conflicts is the allocation between growth and reproduction. In long-lived colonies, for example, workers may favor greater allocation to sexuals than does the queen (Bourke & Franks 1995). The outcome may not be that which most favors the plant. The plant may have very little control, even indirectly, over the proportion of plant-derived resources invested in workers (of potential benefit to the plant) and in dispersing sexuals (only costs to the plant).
5. How do species coexist in the "simple" communities represented by a guild of plant-ants that share a population of hosts (Palmer et al. 2002, Young et al. 1997, Yu & Davidson 1997)? Studies thus far have identified a number of niche dimensions where differences among species may facilitate coexistence. Which of these are most important? How do traits of social

organization influence outcomes of ant interaction with plants, and with competing ants? What coevolutionary dynamics characterize spatially structured populations of interacting ants and plants (Yu et al. 2001)?

Studies integrating processes at local scales and at the scale of interacting metapopulations are now required to deepen our understanding of how these systems evolve, and how they can persist faced with human-induced habitat fragmentation and other global change.

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